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BENTHIC FAUNAL CHANGES IN A SEASONAL ESTUARY OF SOUTH-WESTERN AUSTRALIA

Philip N. Chalmer*
Ernest P. Hodgkin*

and

George W. Kendrick†

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ABSTRACT

The estuary of the Swan River is located in a region of Mediterranean-type climate and experiences contrasting hydrologic conditions from summer to winter. Consequently few species of benthic fauna are able to live there continuously. Data on the occurrence and distribution of benthic fauna over the period 1952-1975 are presented in relation to hydrologic conditions. Distributions within the estuary during and after a two-year period of reduced winter flooding are compared.

INTRODUCTION

The Swan Estuary receives discharge from one of the larger catchment basins of south-western Australia, referred to by Bettenay and Mulcahy (1972) as the Avon System. Most of this System drains the modified agricultural land of the eastern, central and southern wheatbelt, but the western part includes substantially unmodified forest tracts of the Darling Range. The estuary forms the central landscape feature of the Perth Metropolitan Region. Recent district maps of the surface geology have been prepared by Low and Lake (1970) and physiographic and hydrologic aspects of the estuary have been described by Somerville (1921), Aurousseau and

*Department of Zoology, University of Western Australia, Nedlands, W.A. 6009.

†Department of Palaeontology, Western Australian Museum, Perth, W.A., 6000.

Budge (1921), Jutson (1950), Rochford (1951), Spencer (1956), Churchill (1959) and Wilson (1968, 1969).

A two-part division of the Swan Estuary was adopted by Spencer (1956) and Wilson (1968), who envisaged an upper and lower estuary, above and below Heirisson Island. This study suggests that, as a biotope, the estuary divides appropriately into three parts (fig. 1). The Upper Estuary, above Heirisson Island, corresponding to those of Spencer and Wilson, has the character of a tidal river with a meandering channel of fluviatile aspect. The banks are chiefly alluvium, although quartz dune sands are present in places below Guildford. The bed substratum grades from coarse, mainly quartz sand in the upper reaches to dark grey mud downstream. Water depths range from less than 2 metres above Middle Swan to about 6 metres near Maylands. The Canning Arm from Salter Point to Riverton Weir resembles the Upper Estuary of the Swan in its hydrology but has extensive shallow mud and sand flats.

The Middle Estuary, of delta-basin form, extends from Heirisson Island to Blackwall Reach, occupying a wide, drowned valley with extensive shallows in Perth Water and a deep central basin with marginal sand flats in Melville Water. The banks are composed of Pleistocene quartz sands of low relief and discontinuous, more elevated deposits of aeolian calcarenite, the so-called "Coastal Limestone". The Middle Estuary deepens seaward from about 1 metre in parts of Perth Water, to a maximum of 21 m in Mosman Bay. Marginal flats and spits are sandy and support extensive growths of the seagrass *Halophila ovalis*. This plant does not extend into the Upper Estuary. The basin substratum consists of a fine, dark grey mud. In addition, extensive fossil shell beds of Middle Holocene age occur in much of Perth and Melville Waters (Reath, 1925; Serventy, 1955). Combined dredging and foreshore reclamation have greatly modified many areas of both Upper and Middle Estuaries.

The Lower Estuary, from Blackwall Reach to Fremantle Harbour, is an inlet occupying a narrow, winding channel that has been incised through a prominent ridge of Coastal Limestone, forming cliffs which in some places extend below sea level. In contrast to the Middle Estuary, the Lower Estuary shallows seaward from about 16 m near Chidley Point to 5 m or less upstream from the Fremantle road bridges. Here, an extensive sand sill occurs, restricting the flow of both tidal and flood water. The harbour at the mouth of the estuary has been dredged to a depth of 11 m. Substrates range from a fine, dark grey mud in the Blackwall Reach channel to coarse shell and pebble beds in the Rocky Bay channel; elsewhere sand flats and sills predominate. *Halophila ovalis* and *Zostera mucronata*, both seagrasses, occur in shallow areas.

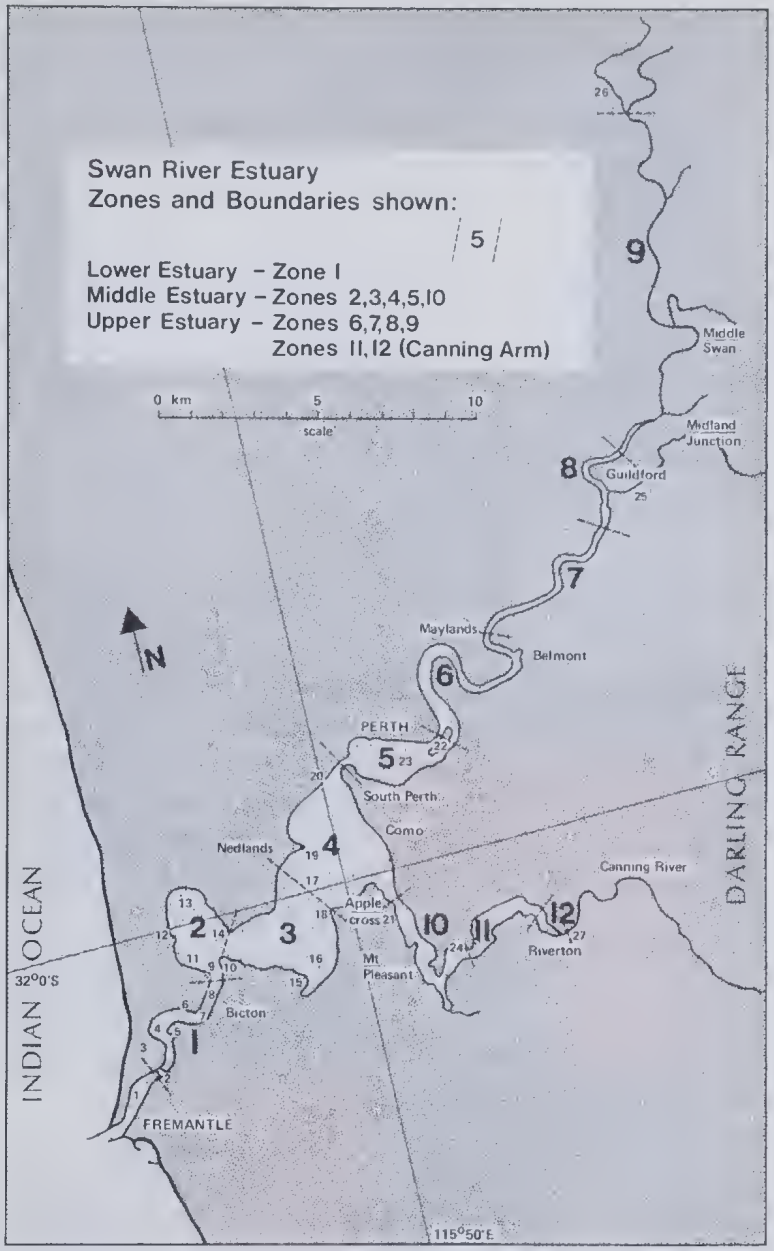


Fig. 1. Swan River Estuary, localities.

1. Fremantle Harbour. *Lower Estuary*. 2. Fremantle bridges. 3. North Fremantle. 4. Rocky Bay. 5. Preston Point. 6. Minim Cove. 7. Point Roe. 8. Blackwall Reach. *Middle Estuary*. 9. Chidley Point. 10. Point Walter. 11. Mosman Bay. 12. Peppermint Grove. 13. Freshwater Bay. 14. Point Resolution. 15. Point Waylen. 16. Lucky Bay. 17. Melville Water. 18. Point Dundas. 19. Pelican Point. 20. Swan Brewery. 21. Canning Bridge. 22. Heirisson Island (Causeway). 23. Perth Water. 24. Salter Point. *Upper Estuary*. 25. Helena River. 26. Ellen Brook. 27. Riverton Weir.

Spencer (1956) has described an annual hydrologic cycle in the Swan Estuary. The two phases of this cycle contrast markedly and are a result of the contrasting summer drought and heavy winter rainfall of the Mediterranean-type regional climate. River discharge ceases during the summer, when the Lower and Middle Estuaries become a virtual arm of the sea. Marine water circulation, induced by a weak tidal oscillation, which may be negated or augmented in effect by changes of barometric pressure, characterises the summer-autumn phase. During winter, river discharge resumes, diminishing or even eliminating tidal influence and introducing comparatively fresh, turbid water into the estuary. A substantial fall in chlorinity, cooling, stratification, light penetration and some de-oxygenation of deep water are among the consequences of this change of phase. These conditions persist until a slackening river discharge in the spring allows marine influences to be reasserted. The Lower Estuary is the last to be affected by the river discharge and the first to which marine influences are restored. Conversely, the Upper Estuary is first to receive floodwater and the last to be penetrated by marine water in summer.

In addition to the two-phase annual cycle, the Swan Estuary experiences widely varying hydrologic conditions from one year to another depending on rainfall and the volume and pattern of river runoff. During the wet years 1963-65 surface water of the Middle Estuary was fresh (<5‰ S.) for four to five months each winter (Bhuiyan, 1966; Wilson, 1968). On the other hand during 1969 salinity was never less than 20‰ and during the winters of 1970-72 it was probably less than 10‰ for only 4 to 6 weeks (E.P.H., unpublished data). The winter of 1973 was moderately wet and salinity was between 5 and 10‰ for about four months. There are no hydrologic data for 1959, but the rainfall record indicates that winter salinities were probably relatively high in that and the three following years. We have used winter rainfall (May to October) for Perth as a convenient, relative measure of the degree of winter river discharge (fig. 2).

Past faunal studies of the Swan Estuary (Thiele, 1930; Thompson, 1946; Serventy, 1955; Wilson, 1964, 1968, 1969; Lucas, 1968, 1971; Lucas and Hodgkin, 1970) have revealed a low species diversity of benthic fauna. This paper presents further results of collections and observations from the Swan Estuary in relation to hydrologic fluctuations over the past 20 years. The information is presented in two parts. Part 1 deals with Western Australian Museum records of the benthic fauna and Part 2 considers distributions of benthic species during two summers, one after a series of dry winters with low rainfall and the other after a wet winter of above average rainfall. Most of the data concern molluscs; other groups, such as polychaetes, crustaceans, echinoderms and coelenterates have been studied less consistently.

For the taxonomy of tapetinine bivalves, Lamy (1922) and Fischer-Piette and Métivier (1971) have been followed; for oysters, Stenzel (1971); for Pinnidae, Rosewater (1961); for *Proxichione*, Darragh (1965) and for other bivalves, Part N of the Treatise on Invertebrate Paleontology has been used as a guide.

Part 1. Museum records

The records of molluscs, echinoderms and coelenterates presented below are drawn from the collections of the Western Australian Museum. With the exception of a few earlier records, they are the results of collecting by many persons, including the present writers, since the early 1950s. Further supplementary data are provided in Part 2 of this paper.

Collecting was most intensive in the more accessible, marginal habitats. Sand flats were sampled by sieving and rocky areas were examined intertidally and in the shallow sub-littoral; rocks were turned over and crevices and borings searched. Submerged wood was similarly investigated, particularly in the Upper Estuary. Areas of algal growth, sea grass and rushes were sampled directly and by sieving and dredging. The deeper basins and channels were collected with a towed dredge, the recovery (pebbles, sand and mud) being sieved and sorted mainly in the boat; sorting of some finer substrates was completed under magnification in the laboratory. Most collecting activity took place in the summer-autumn period, but a proportion was carried out at other times of the year.

The sectional (i.e., Upper, Middle or Lower) faunas of the estuary were each divided into continuous and temporary resident species. Continuous status was accepted in cases where living specimens had been collected or observed regularly throughout the year and the maturity of individuals indicated prolonged residence in the locality. A few species, known only from specimens collected dead, were also assessed as continuous residents. These were obtained in fresh condition (e.g., containing soft tissue remnants or having a fresh periostracum) and usually by deep water dredging. Such species are deep substrate burrowers and the failure to collect living examples may be a consequence of inadequate sampling techniques.

A species was assessed as a temporary inhabitant of a zone if records, living or dead, were sporadic or if evidence of mature specimens regularly present in the area was lacking. Future dredging in the deeper parts of the estuary may reveal that some burrowing species regarded as temporary residents are actually continuous and *vice versa*; this applies mainly to some records from the Lower Estuary. All occurrences are based on positive records; inferred distributions have not been included in the tables of results.

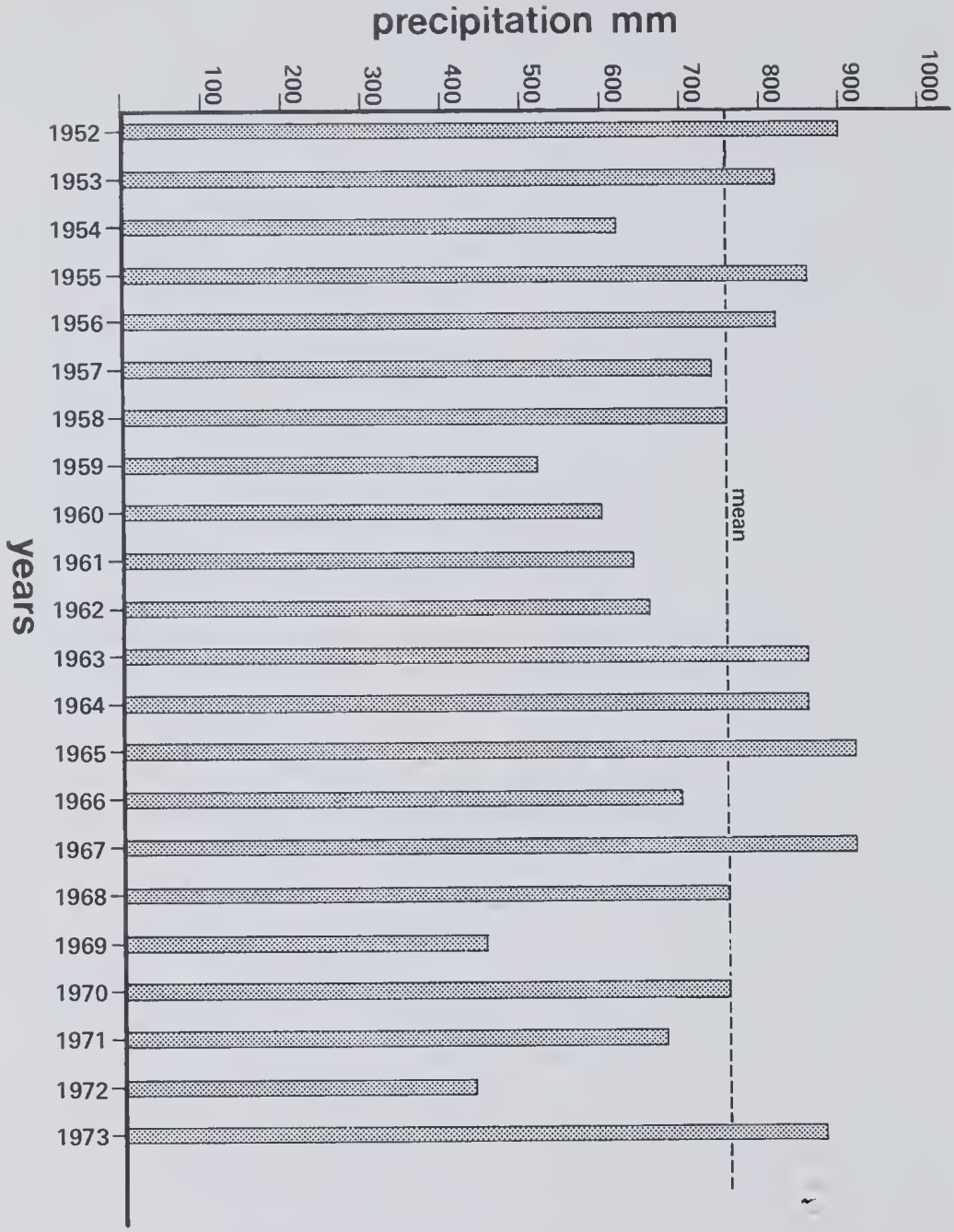


Fig. 2. Total precipitation (mm) at Perth for the six wettest months, May to October inclusive, 1952 to 1973. Mean is for the hundred years 1876 to 1975.

Results. Table 1 lists the benthic fauna according to the presence or absence of each species on a continuous or temporary basis in each of the three sections of the estuary. A local marine presence for each species is also indicated where appropriate, based on Museum collection data. The table is followed by a more detailed discussion of the habitat and other field observations of most species.

Table 1. Distributions of benthic molluscs, echinoderms and coelenterates within the Swan Estuary; marine occurrences of species are given where available. A cross (+) in the columns for estuarine records indicates that one or more live-collected specimens are known. An asterisk (*) indicates that the record is based on dead material.

SPECIES	Marine records (W.A.)	Lower Estuary		Middle Estuary		Upper Estuary	
		Temp.	Cont.	Temp.	Cont.	Temp.	Cont.
MOLLUSCA							
AMPHINEURA							
Acanthochitonidae							
1. *Acanthochiton* sp.		+					
Lepidopleuridae							
2. Lepidopleurid, genus uncertain		+					
BIVALVIA							
Solemyidae							
3. *Solemya (Solemyarina) australis* Lamarck	+			*			
Mytilidae							
4. *"Amygdalum" glaberrimum* (Dunker)	+	+					
5. *Brachidontes* sp. cf. *B. variabilis* Krauss	+	+					
6. *Musculus paulucciae* (Crosse)	+	+					
7. *Musculus* sp. cf. *M. nanulus* Thiele		+					
8. *Mytilus edulis planulatus* (Lamarck)	+		+	+			
9. *Xenostrobus pulex* (Lamarck)	+		+				
10. *Xenostrobus securis* (Lamarck)		+			+		+
Pinnidae							
11. *Pinna bicolor* Gmelin	+	*		*			
Pteriidae							
12. *Pinctada fucata* (Gould)	+	+					
Malleidae							
13. *Malleus meridianus* Cotton	+		+				

Table 1 Continued

SPECIES	Marine records (W.A.)	Lower Estuary		Middle Estuary		Upper Estuary	
		Temp.	Cont.	Temp.	Cont.	Temp.	Cont.
Pectinidae							
14. *Chlamys asperrimus* (Lamarck)	+	*		*			
Anomiidae							
15. *Anomia descripta* Iredale	+		+	*			
Ostreidae							
16. *Saccostrea cuccullata* (Born)	+	+		*			
Lucinidae							
17. *Cavatidens perplexa* (Cotton and Godfrey)	+	+					
18. *Wallucina assimilis* (Angas)	+	*		*			
19. *Wallucina* sp.	+	*		+			
20. *Epicodakia* sp.	+	*					
Ungulinidae							
21. *Felaniella* (*Zemysia*) sp.		+					
Chamidae							
22. *Chama ruderalis* Lamarck	+		+				
Erycinidae							
23. *Arthritica semen* (Menke)		*			+	+	
Kelliidae							
24. *Kellia australis* (Lamarck)	+	+					
25. *Marikellia* sp.		+					
Leptonidae							
26. *Lepton* sp.		+					
Montacutidae							
27. *Mysella* sp.		*					
Carditidae							
28. *Megacardita incrassata* (Sowerby)	+		+				
Cardiidae							
29. *Laevicardium* (*Fulvia*) *apertum* (Bruguiere)	+	+		*			
Mactridae							
30. *Mactra* (*Electomactra*) *antecedens* (Iredale)	+	+		*			
31. *Spisula* (*Notospisula*) *trigonella* (Lamarck)	+ rare		+		+	*	
Mesodesmatidae							
32. *Mesodesma angusta* Reeve	+	+					
Cultellidae							
33. *Phaxas* (*Ensiculus*) *cultellus* (Linnaeus)	+		+	*			

Table 1 Continued

SPECIES	Marine records (W.A.)	Lower Estuary		Middle Estuary		Upper Estuary	
		Temp.	Cont.	Temp.	Cont.	Temp.	Cont.
Tellinidae							
34 *Tellina* (Macomona) *deltoidalis* Lamarck	+		+		+	*	
35. *Tellina (Pharaonella) perna* Spengler	+	*					
36. *Tellina (Pinguitellina)* sp.	+		+				
37. *Tellina (Tellinangulus)* sp.	+	+					
38. *Tellina* sp.	+	*					
Psammobiidae							
39. *Sanguinolaria (Psammotellina) biradiata* (Wood)	+		+				
Semelidae							
40. *Theora (Endopleura) lubrica* Gould	+				+		
Veneridae							
41. *Chioneryx cardioides* (Lamarck)	+	+		*			
42. *Circe sulcata* Gray	+	*		*			
43. *Dosinia (Pectunculus) sculpta* (Hanley)	+	*					
44. *Gomphina undulosa* (Lamarck)	+	+					
45. *Paphia (Callistotapes) crassisulca* (Lamarck)	+		+				
46. *Irus (Irus) carditoides* (Lamarck)	+	+					
47. *Irus (Irus) crenata* (Lamarck)	+		+	+			
48. *Irus (Notirus) iridescens* (Tate)	+	+					
49. *Proxichione laqueata* (Sowerby)	+	*					
50. *Venerupis anomala* (Lamarck)	+	+					
Petricolidae							
51. *Petricola (Velargilla)* sp.	+	*					
Hiatellidae							
52. *Hiatella australis* (Lamarck)	+	+					
Lyonsiidae							
53. *Anticorbula amara* (Laseron)		*			+		+
GASTROPODA							
Acmaeidae							
54. *Acmaea (Notoacmea) onychitis* (Menke)	+	+					

Table 1 Continued

SPECIES	Marine records (W.A.)	Lower Estuary		Middle Estuary		Upper Estuary	
		Temp.	Cont.	Temp.	Cont.	Temp.	Cont.
Trochidae							
55. *Monilea callifera* (Lamarck)	+	*					
Cyclostrematidae							
56. *Elachorbis tatei* (Angas)	+	*					
Littorinidae							
57. *Bembicium melanostomum* (Gmelin)	+		+				
58. *Littorina (Austrolittorina) unifasciata* Gray	+	+					
Hydrobiidae							
59. *Hydrococcus graniformis* Thiele	rare - see text	last recorded about 1840					
60. *Potamopyrgus* sp.		*					+
61. *Tatea preissi* (Philippi)		*			+		+
Assimineidae							
62. *Assiminea* sp.							+
Tornidae							
63. *Teinostoma* sp.		*					
64. *Vitrinella* sp.		*					
Rissoidae							
65. *Alvinia (Linemera)* sp.		*					
66. *Ovirissoa nitidula* (Thiele)	+	+					
Thiaridae							
67. *Plotiopsis australis* (I. & H.C. Lea)							+
Potamididae							
68. *Batillaria (Velacumantus) australis* (Quoy & Gaimard)	+		+		+		
Diastomatidae							
69. *Obtortio* sp.	+	+					
Cerithiidae							
70. *Alaba fragilis* (Thiele)	+		+				
71. *Alaba pusilla* (Thiele)	+	*					
72. *Diala lauta* (A. Adams)	+	*					
Epitoniidae							
73. *Epitonium* sp. cf. *E. imperiale* (Sowerby)	+	+					
Muricidae							
74. *Trophon (Bedeva) paivae* Crosse	+		+	+			

Table 1 Continued

	Marine records (W.A.)	Lower Estuary		Middle Estuary		Upper Estuary	
		Temp.	Cont.	Temp.	Cont.	Temp.	Cont.
Columbellidae							
75. *Milrella (Denlimilrella) lincolnensis* (Reeve)	+	*					
76. *Zafra vercoi* (Thiele)	+	+					
Nassariidae							
77. *Nassarius burchardi* (Philippi)	+		+		+	*	
78. *Nassarius pauperatus* (Lamarck)	+		+		+		
79. *Nassarius pauperus* (Gould)	+		+				
80. *Nassarius pyrrhus* (Menke)	+	+					
Pyramidellidae							
81. *?Aclis* sp.		+					
82. *Syrnola bifasciata* (Tenison Woods)		+					
83. *Turbonilla (Pyrgiscus) fusca* (A. Adams)	+	*					
Bullidae							
84. *Bulla lenuissima* Sowerby	+	+					
Atyidae							
85. *Liloa brevis* (Quoy & Gaimard)	+	+					
Akeridae							
86. *Akera solula* (Gmelin)	+	+					
Scaphandridae							
87. *Acleocina* sp. cf. *A. canaligradala* Ludbrook		+					
88. *Adamneslia arachis* (Quoy & Gaimard)	+	+					
89. *Roxania hordeacea* (A. Adams)		*					
Philinidae							
90. *Philine angasi* (Crosse & Fischer)	+		+	*			
91. *Philine* sp.			+	+			
Aglajidae							
92. *Aglajid*, cf. *Nakamigawaia* sp.		+					
Aplysiidae							
93. *Aplysia angasi* Crosse & Fischer	+	+					
94. *Aplysia* sp.	recorded in Part 2						
Elysiidae							
95. *Elysia australis* (Quoy & Gaimard)	+	+					

Table 1 Continued

	Marine records (W.A.)	Lower Estuary		Middle Estuary		Upper Estuary	
		Temp.	Cont.	Temp.	Cont.	Temp.	Cont.
Siphonariidae							
96. *Siphonaria baconi* Reeve	+	+					
97. *Siphonaria luzonica* Reeve	+	+					
ECHINODERMATA							
ECHINOIDEA							
Temnopleuridae							
98. *Temnopleurus michaelseni* (Döderlein)	+		+				
Laganidae							
99. *Peronella lesueri*	+	+		+			
Loveniidae							
100. *Breynia australasiae* (Leach)		+			*		
STELLEROIDEA							
Astropectinidae							
101. *Astropecten triseriatus* Muller & Troschel	+	+					
Oreasteridae							
102. *Anthenea australiae* Döderlein	+	+					
Ophiactidae							
Ophiactis sp. cf. *O. acosmeta* H.L. Clark			+				
Amphiuridae							
104. *Amphipholis squamata* (Della Chiaje)	+		+				
105. *Amphiura* sp. cf. *A. constricta* Lyman			+				
COELENTERATA							
ANTHOZOA							
Veretillidae							
106. Seapen, unidentified	+		+				
Rhizangiidae							
107. *Culicia* sp. cf. *C. tenella* Hoffmeister	+	+					
Stoichactidae							
108. *Radianthus concinnata* Lager	+	+					

Remarks on individual species

The two amphineuran species are known only from channel dredgings around Rocky Bay. All specimens are small and uncommon.

Mytilus edulis planulatus. A large colony lived on the piles of the old Fremantle railway bridge until its demolition in 1966; subsequently this

species has been recorded living upstream to Bicton, and from 1970 to the winter of 1973, temporarily in the Middle Estuary upstream to Pelican Point (E.P. Hodgkin, unpublished data). This species was common on pilings at Pelican Point during the summers of 1960-64 but was severely affected by the winter floods (Wilson, 1964: 73-4).

Brachidontes sp. cf. *B. variabilis.* At Rocky Bay, recently-dead juveniles were common on intertidal rocks in Dec. 1960 and were living there also in Mar. 1973. Each record follows a dry winter.

"Amygdalum" glaberrimum. A mature, living specimen was dredged from a sand-flat, now removed, upstream from the old Fremantle railway bridge in Dec. 1964; juveniles were living on the Rocky Bay sand flat in Jan. 1973.

Xenostrobus securis were collected from the Lower Estuary in a recently-dead condition at Preston Point in Dec. 1964 and living at Minim Cove in Jan. 1974. Wet winters preceded both of these records. Occurrences in the Lower Estuary appear to be sporadic and those in the downstream part of the Middle Estuary probably have been temporary. The species is a continuous inhabitant in the upstream part of the Middle Estuary and in the Upper Estuary to about Midland Junction and Riverton, forming mat-like colonies on submerged objects such as piles, logs and rocks. There are no marine records of the species from Western Australia. Adults are tolerant to a wide range of salinities but fertilisation and larval development can occur only within a limited salinity range (Wilson, 1968). This evidently precludes establishment of colonies in either the sea or in the uppermost extremities of the estuary. The related *X. pulex* also occurs in the Lower Estuary and care is needed in distinguishing between the two species. *X. securis* is doubtless that species collected at Perth and Canning River in 1905 by the Hamburg Expedition and listed as *Modiolus pulex* by Thiele (1930).

X. pulex. Mature specimens that appear to have lived through a winter were occasionally found intertidally on rocky substrates downstream from Blackwall Reach.

Pinna bicolor. Empty shells, some in fresh condition, were collected from the Rocky Bay channel in 1960, 1973 and 1974 and from Freshwater Bay in 1962. All are small and appear to represent temporary colonisations.

Malleus meridianus and *Chama ruderalis.* Mature specimens of both species have been found regularly in channel dredgings downstream from Pt Roe.

Pinctada fucata. A well-grown living specimen was dredged from Rocky Bay in June 1962.

Anomia descripta. Mature living specimens were common at Rocky Bay in the channel and on deeper sand flats and less frequently attached to rocks in the shallow sub-littoral. Some articulated valves, one with attached muscle tissue, were washed ashore at Perth Water (South Perth) in Apr. 1970 and may represent a temporary incursion into the Middle Estuary following the dry winter of 1969.

Saccostrea cucullata. This rock oyster was not uncommon in the littoral and sub-littoral around Rocky Bay and occasionally upstream to Freshwater Bay. All individuals and colonies are small and appear to have been short-lived.

Wallucina assimilis. Fresh valves of this species, including articulated pairs, were present in dredged sandy substrates of the Lower Estuary in January of 1973 and 1974. No living record has been obtained. *W. assimilis* appears to be less common than the following species, which is distinguished by a more robust, rounded shell with stronger concentric sculpture.

Wallucina sp. Articulated pairs of valves were common in dredged sandy substrates of the Lower Estuary between Jan. 1973 and Mar. 1974. A single living specimen was dredged from Melville Water near Pt Walter in Jan. 1963. This record follows a dry winter.

Arthritica semen. This minute clam was abundant on sand flats of the Middle Estuary and ranged into the lower reaches of the Upper Estuary. Occurrences in the Lower Estuary were sporadic; there are no marine records from Western Australia. Ashman (1969) indicates that this species tolerates salinities ranging from normal sea water to 2‰ S.

Megacardita incrassata occurs living in the deeper parts of Rocky Bay and in the Blackwall Reach channel. Specimens are of mature size and suggest a continuous population.

Mactra (Electomactra) antecedens was a common species living on the Rocky Bay sand flat in Feb. 1960 and Jan. 1961 but was not observed again until Dec. 1973. These records follow dry winters.

Spisula (Notospisula) trigonella. The sudden appearance of this species in the Swan Estuary around 1964 was recorded by Wilson and Kendrick (1968). Since then, it has become a continuous and conspicuous inhabitant of the sand flats in the Lower and Middle Estuaries; it is also present in the deeper basins and channels of the Middle Estuary. In periods of reduced river discharge, this species expands temporarily upstream to Belmont and Riverton. Western Australian marine records are rare.

Phaxas (Ensiculus) cultellus. Though never common, recently-dead, articulated shells of this species are regularly found in dredgings from the Lower Estuary, suggesting that a continuous population may be present. Recently-dead specimens from Melville Water near Pt Walter in the summer

of 1962-63 are believed to represent a temporary incursion into the Middle Estuary similar to that of *Laevicardium apertum* in the same period. A mature, living specimen was collected at North Fremantle in Jan. 1974.

Tellina (Macomona) deltoidalis was commonly found living on the Rocky Bay sand flat in Feb. 1960 and Jan. 1961 and since then has been collected regularly, either living or in a recently-dead condition, from the sand flats of the Lower Estuary, where it appears to be a continuous resident. Other records, living and recently dead, from Pt Waylen, May 1953, Heirisson Island, May 1953 and Pt Walter spit, Apr. 1960, suggest that it invades the Middle Estuary in the summer but does not regularly survive the winter phase of the hydrologic cycle. A single old valve from Belmont, Oct. 1966, indicates a temporary extension into the Upper Estuary, probably following an interval of reduced river discharge. It is occasionally collected in the sea near Fremantle.

Tellina (Pharaonella) perna. A dead, articulated juvenile shell from the Rocky Bay sand flat in the summer of 1959-60 appears to represent a temporary incursion into the Lower Estuary as a result of the dry winter of 1959.

Tellina (Pinguitellina) sp. Mature, living specimens were collected from the Rocky Bay channel and sand flat in Jan. 1974, following the normal winter rainfall of 1973.

Tellina sp. This is a pink, thin-shelled tellin of undetermined subgenus; recently-dead valves, some articulated, were collected from the channel of the Lower Estuary in 1973 and 1974.

Sanguinolaria (Psammotellina) biradiata. Several live records and other recently-dead specimens collected from Preston Point and North Fremantle over 1971-73 indicate a continuous population in the Lower Estuary. This species burrows deeply into the substrate and is not readily collected alive.

Theora (Endopleura) lubrica. Live specimens were dredged from mud in 4 m at Lucky Bay, Feb. 1973 and Mar. 1974 and from Freshwater Bay in Mar. 1974. It was abundant on each occasion and appears to be well established in the basin and channel areas of the Middle Estuary. The only other record of this species known to us from Western Australia is from a beach near Rockingham, May 1971. It appears that the species may be a recent addition to the benthos of the Swan Estuary, comparable with *Spisula (Notospisula) trigonella* discussed previously. *T. (E.) lubrica* has recently been reported for the first time from places as far apart as California (Seapy, 1974) and New Zealand (Powell, 1974) and appears to have expanded considerably beyond its previously-known range along the Pacific coast of Asia (Kuroda *et al.*, 1971 : 447).

Proxichione laqueata. A recently-dead single juvenile valve was found in Jan. 1961 and a large single valve in poor condition was dredged in Jan. 1973. Both specimens were collected at Rocky Bay.

Dosinia (Pectunculus) sculpta. Recently-dead, articulated pairs of valves were common on the Rocky Bay sand flat in the summer of 1960-61 and may have lived during the dry winter of 1959. Numerous other recently-dead specimens have been collected from around Rocky Bay since then but no living specimen is yet known. The only local marine record known to us is an articulated pair of valves in fresh condition collected at Rockingham in 1940; the species is common at Shark Bay and other northern localities.

Circe sulcata. As with the preceding, there are several records of this species, comprising recently-dead, articulated shells from the Lower Estuary over the period 1960-75, but no living specimen has yet been obtained. Some recently-dead, articulated specimens were also dredged from Melville Water near Pt Walter in Oct. 1962 and Jan. 1963. This species was collected in 1905 by the Hamburg Expedition in Freshwater Bay and listed by Thiele (1930) as *Circe lentiformis* sp. nov. The Thiele type is of fresh appearance and may have been collected living (R. Kilias, pers. comm.).

Paphia (Callistotapes) crassisulca. Recently-dead articulated specimens, some of mature size, were dredged from the deeper parts of Rocky Bay in Jan. 1973, Jan. and Mar. 1974. A living juvenile was obtained in Mar. 1974.

Irus (Irus) crenata was common throughout the Lower Estuary living on sand flats, in rock cavities and in channel beds. Shells from rock cavities tend to be of irregular shape. Living records from Pt Dundas, Dec. 1972 and Applecross, Nov. 1972 suggest a temporary occupation of the lower part of the Middle Estuary following the previous dry winter. Other non-living records from Canning Bridge and the Causeway, both 1961, point to temporary settlement further upstream when conditions are favourable.

Irus (Irus) carditoides and *Irus (Notirus) iridescens* were collected alive from the Rocky Bay sand flat in the summer of 1959-60, while *Venerupis anomala* was also living there then and in the following summer. An empty, articulated shell of *Petricola (Velargilla)* sp. was collected from the same place in Jan. 1961. These records follow the dry winters of 1959-60; none of the species has since been re-collected from the estuary.

Anticorbula amara. This appears to be the species collected at Guildford in 1905 by the Hamburg Expedition and listed by Thiele (1930) as *Modiolus (Fluviolanatus) subtortus* (Dunker). Lower Estuary records are infrequent and the species appears to be temporary there. *A. amara* can live at marine salinities (E.P.H., unpublished data) but there are no known marine occurrences from Western Australia. The species is continuous in the

Middle and Upper Estuaries and collecting in recent years has established that it inhabits the Swan-Avon River upstream to beyond York. This non-estuarine population appears to have become established over the past 50 years and its establishment coincides with pronounced hydrologic changes, mainly increased salinity, in the Avon River (Kendrick, 1976). Such changes have been attributed to the clearing of land for agriculture (Peck and Hurle, 1973). The species lives attached by byssal threads to submerged, firm substrates, large sand grains and aquatic plants.

An assortment of gastropods, *Acmaea (Notoacmea) onychitis*, *Littorina (Austrolittorina) unifasciata*, *Epitonium* sp. cf. *E. imperiale*, *Siphonaria luzonica* and *S. baconi*, were all collected alive from the Rocky Bay-Preston area in the summer of 1973-74. *A. (N.) onychitis* (empty shells in growth position) was also found at Preston Pt in Dec. 1960. These records all follow dry winters.

Bembicium melanostomum is common on intertidal rocks from Blackwall Reach downstream. In Western Australia, this species is mainly confined to estuaries, although a small marine population occurs on the south side of Woodman Point near Fremantle. Thompson (1946) recorded a "*Trochus* sp." in abundance along the littoral of Freshwater Bay. The identity of this species is uncertain but it may have been *B. melanostomum*, which has a trochiform shell. If so, there appears to have been a contraction of range downstream within the last 30 years.

Tatea preissi was first collected by Preiss from the Swan Estuary about 1840 and described by Menke (1843) under the preoccupied name *Paludina acuta*. Our earliest subsequent records are dead shells from Peppermint Grove, 1927 and from Bicton and Belmont, 1956. It was found living among mat colonies of *Xenostrobus securis* at the Causeway, Nov. 1969 and was common, living on intertidal rocks at Pt Walter, Pt Dundas and Peppermint Grove, Apr. 1970. This species appears to be a continuous inhabitant of the intertidal of the Middle Estuary and upstream to about Guildford; no marine or fluviatile records are known from Western Australia.

Hydrococcus graniformis was initially collected by Preiss around 1840 from "among white quartz sand on the bank of the Swan River" (Smith, 1882). Menke (1843) described these specimens under the preoccupied name *Paludina granum*. Thiele (1928) re-named and further described the Preiss-Menke specimens, adding details of the anatomy, indicating that they were collected alive. In all probability, they originated (together with Preiss' specimens of *Arthritica semen*), from a marginal sand flat of Melville Water in the Middle Estuary. Since the initial discovery, no living specimen of *H. graniformis* has been recorded from the Swan. Observations of the

species in other estuaries of south-western Australia (e.g., Leschenault, Hardy and Nornalup Inlets) show that the preferred habitat is on shallow sand flats. In the Middle Estuary of the Swan, this habitat has been considerably modified over recent decades by extensive dredging and shore reclamation. Empty shells of *H. graniformis*, none of fresh appearance, are common in fine substrates of the Lower and Middle Estuaries. They do not appear to have lived recently and it appears not unlikely that the species is now extinct in the Swan. There are no fluviatile or marine records from south-western Australia but the species is common in parts of Shark Bay; its listing as a freshwater element by McMichael (1967) is incorrect.

Potamopyrgus sp. Old shells of this species have been occasionally found in fine substrates from the Rocky Bay area but only recently (Mar. 1975) have living specimens been found. These were located in the Canning Arm at Riverton on sand flats and among rushes of a largely unmodified area. The species inhabits other estuaries in south-western Australia but there are no wholly marine or fluviatile records.

Assiminea sp. Living specimens were found together with *Potamopyrgus* sp. amongst rushes in the Canning Arm, Riverton, March 1975. Both of these species may have been overlooked previously because of their now-restricted habitat, which has been progressively eliminated by dredging and reclamation.

Plotiopsis australis is the only mollusc species of freshwater affinity known to occur in the estuary. It can survive salinities up to 25‰ (Blackwell, 1969) and is common in the Upper Estuary above Guildford. The species occurs in rivers of northern Western Australia, south to the Swan-Avon.

Batillaria (Velacumantus) australis. Since 1960, this species has been collected regularly from the Lower Estuary and the lower part of the Middle Estuary, where it occurs in abundance. Empty shells from the Canning at Mt Pleasant, Apr. 1972 and living specimens from Canning Bridge, Dec. 1972 suggest temporary range extensions upstream following periods of reduced river discharge.

Alaba fragilis was common living on a weed-grown part of the Rocky Bay sand flat in Jan. 1973 (following the dry winter of 1972), but living specimens were rare at the same station one year later. Freshly-dead specimens were obtained in the same general area in 1956 and 1963. The type material was collected at Freshwater Bay (Thiele, 1930).

Trophon (Bedeva) paivae. Common on the sand flats, rocky shores and channel throughout the Lower Estuary. Freshly-dead shells and occasional living specimens have been found in Freshwater Bay and Melville Water near Pt Walter.

Zafra vercoi and *?Aclis* sp. were both common species living on the Rocky Bay sand flat in Jan. 1973 but only empty shells of each species were collected at the same station in Jan. and Mar. 1974. Evidently the species became established in the Lower Estuary following the dry winter of 1972 but could not survive the winter of 1973.

Nassarius pauperatus. Mature specimens, both living and recently-dead, have occasionally been found on the sand flats of the Lower Estuary; living specimens have also been collected at Pt Resolution, Mar. 1969, and Pelican Pt, Mar. 1973. Smith (1975) has established that 12 to 18 months are required for this species to reach maturity. It appears therefore that specimens collected would have survived at least one winter in either the Middle or Lower Estuaries.

Nassarius burchardi is a continuous inhabitant of sand flats and deeper areas throughout the Lower and Middle Estuaries, where it is one of the most abundant gastropods. Empty shells from Belmont, Dec. 1970, suggest a temporary move into the Upper Estuary, perhaps following the dry winter of 1969. Over the period 1972-74, *N. burchardi* was killed during the winters in shallow waters at the upper limits of range, but was able to survive in deeper, more saline waters in the same general area (Smith, 1975). From the Swan, the species is known only since about 1965, when the initial records were made. It was not observed during intensive collecting of the Rocky Bay-Pt Walter area in 1959-63, although the much rarer *N. pauperatus* was collected twice in that period. The first appearance and subsequent massive proliferation of *N. burchardi*, a scavenger, coincided with the establishment of *Spisula (Notospisula) trigonella* in the estuary (Wilson and Kendrick, 1968). The two species have a similar distribution within the estuary and the bivalve may be an important food resource for the snail.

Nassarius pauperus. Living and freshly-dead specimens of mature size dredged from the channel of the Lower Estuary on four occasions over 1973-74 suggest a continuous population there.

Philine angasi. Records of living specimens from the Blackwall Reach channel (Jan. 1963, Nov. 1969) and the Rocky Bay sand flat (Jan. 1974) suggest that a continuous population inhabits the Lower Estuary.

Philine sp. was collected from the Rocky Bay sand flat (Jan. 1973, Jan. and Mar. 1974) and in Lucky Bay (Mar. 1974). These are the only known records for the species, which is believed to be undescribed (R. Burn, *pers. comm.*).

Akera soluta was found living on the Rocky Bay sand flat in Jan. 1974 and may be only temporary in the Lower Estuary.

Temnopleurus michaelseni. This echinoid was dredged alive from the Rocky Bay channel in Dec. 1962, Jan. 1963 (from field notes, G.W.K.) and in Jan. 1973; also collected alive from rocks in the sublittoral at Bicton, Apr. 1974.

Breynia australasiae. A freshly-dead test of adult size, devoid of spines but with some of the fragile anal plates intact, was collected at Lucky Bay in Nov. 1961, following the dry winters of 1959-60.

Peronella lesueuri. The first of two records comprises four juveniles, all bearing spines and evidently collected alive. They were collected by members of the Natural History Society (forerunner of the Royal Society of Western Australia) apparently in Dec. 1908 during a dredging excursion between Perth and Chidley Point. A live juvenile of this species was trawled from 8-10 fathoms in Blackwall Reach, June 1962, following a sequence of dry winters.

The ophiuroids *Amphiura* sp., *Ophiactis* sp. and *Amphipholis squamata* were dredged from the Lower Estuary channel below Pt Roe in Jan. 1973 and Mar. 1974.

Astropecten triseriatus was dredged from 7-10 m in Blackwall Reach, July 1970, and was collected in less than 1 m of water on sand at Bicton, Feb. 1971. *Anthenea australis* was collected at Mosman Bay in Jan. 1974 and at Bicton in Apr. 1974. These few starfish records probably represent temporary incursions into the lower parts of the estuary.

The anemone *Radianthus concinnata* was dredged from 4-8 m on the western slope of the Rocky Bay sand bank in Jan. 1973.

Culicia sp. cf. *C. tenella.* A living colony of this small, semi-colonial, ahermatypic coral was dredged from a shingle substrate in the channel of the Lower Estuary near Minim Cove in Mar. 1974. It is indistinguishable in size of colony and growth form from samples of the same species from Garden Island off Fremantle (L.M. Marsh, personal communciation, Oct. 1975).

Part 2. Littoral surveys during the summers of 1972-73 and 1973-74.

Surveys of benthic fauna around the margins of the Swan Estuary were carried out by P.N. Chalmer from Dec. 1972 to Feb. 1973 and during Nov.-Dec. 1973. The first survey followed a period in which three of the four preceding winters had been relatively dry (fig. 2) and winter salinities had remained relatively high (see Introduction). The subsequent winter of 1973 was comparatively wet and the surface salinity in the Middle Estuary was no more than 5‰ for the 6-8 weeks during August-September.

On both surveys, the margins of the estuary within a water depth of one metre were collected. Rocks, logs, piles and beds of sea grass *(Zostera mucronata, Halophila ovalis)* were examined; substrates were washed through a 1 mm sieve. Specimens were identified and recorded on site and most were released. Some of the less common species were deposited in the Western Australian Museum. Common species only are recorded here.

Results. The Lower, Middle and Upper Estuaries were subdivided into 12 zones (fig. 1) to permit a more detailed presentation and analysis of results. Species distributions according to zones on each survey together with habitat preferences are shown in Table 2.

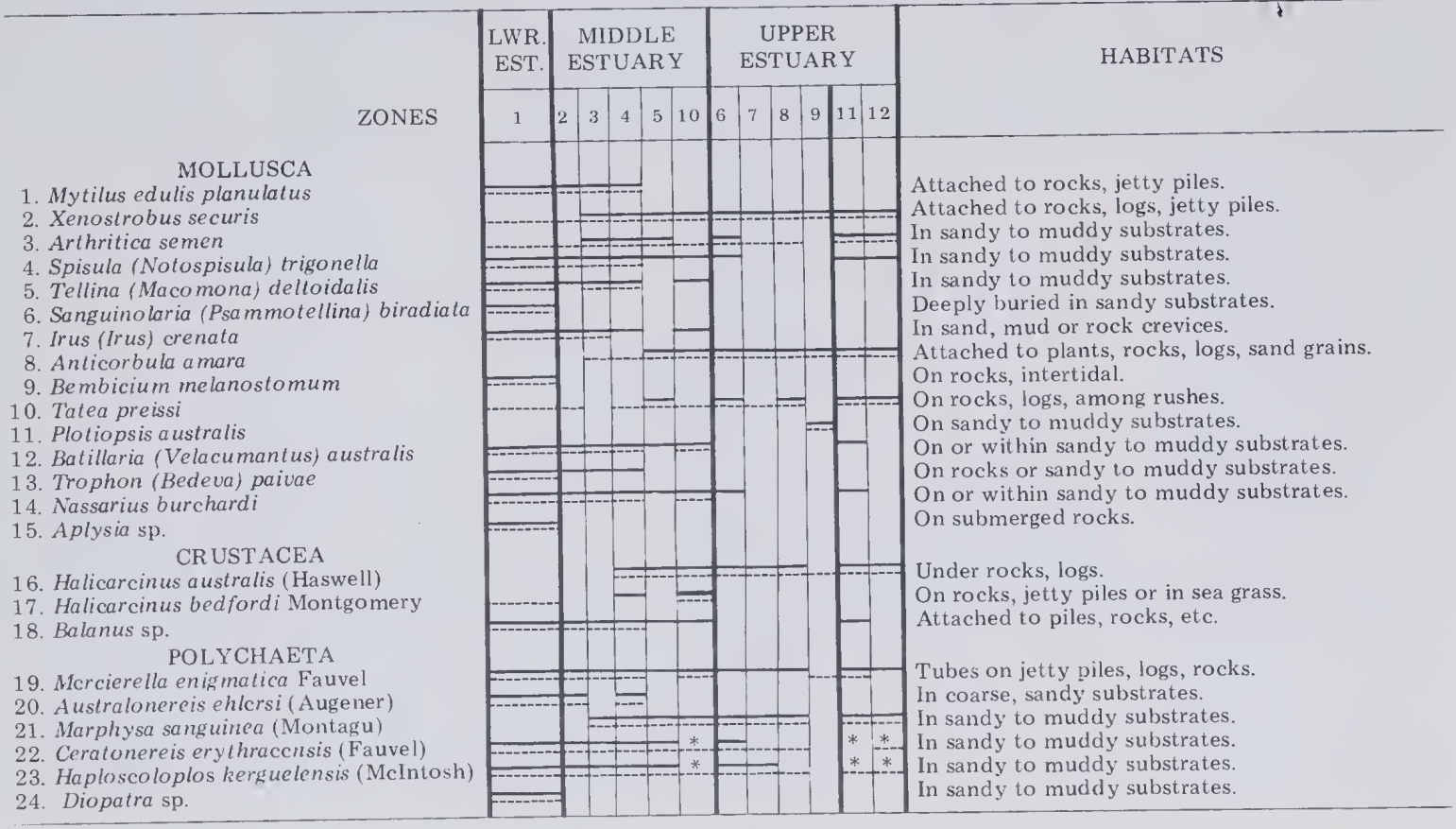
Distributions of four mollusc species, *Sanguinolaria (Psammotellina) biradiata, Bembicium melanostomum, Plotiopsis australis* and *Aplysia* sp. were unchanged on the two surveys. These species occurred at either the upper or lower extremities of the estuary, the parts of greatest hydrologic stability. Four other species, *Xenostrobus securis, Arthritica semen, Tatea preissi,* and *Anticorbula amara,* which are usually associated with the Middle and Upper Estuaries, had extended their ranges downstream, the first three as far as Rocky Bay, by the second survey.

The ranges of the other molluscs, *Mytilus edulis planulatus, Spisula (Notospisula) trigonella, Irus (Irus) crenata, Batillaria (Velacumantus) australis, Nassarius burchardi, Tellina (Macomona) deltoidalis* and *Trophon (Bedeva) paivae,* had contracted downstream by the second survey; on that occasion, only recently-dead shells were found at the previous summer's upstream range limits. The second survey further showed that the first five of these seven species were represented at their upstream limits only by newly-settled juveniles, which had evidently been dispersed as larvae from a downstream source in the estuary. For example, the upstream limit of adult *Mytilus* was at Rocky Bay in the Lower Estuary (zone 1), but newly-settled juveniles were located as far upstream as Nedlands in the Middle Estuary (zone 4). Similarly, on the first survey it was noted that *S. (N.) trigonella* and *N. burchardi* were represented at their upstream limits by juveniles which apparently had extended their ranges upstream as planktonic larvae.

The crab *Halicarcinus bedfordi* maintained its range between the surveys, although it was less common on the second occasion. This species was abundant amongst the sea grass *Halophila ovalis,* the leaves of which died back during the winter of 1973, and the reduced numbers of the crab are considered to be a direct response to the temporary decline of the *Halophila* beds. If so, then the reduced numbers of *H. bedfordi* would have been only an indirect consequence of the winter river discharge. The congenor,

TABLE 2

Records of common benthic fauna living in shallow marginal habitats around the Swan Estuary. For each species, the upper, continuous line shows the distribution observed during the summer of 1972-73. following several dry winters. The lower, broken line shows the distribution observed in the summer of 1973-74, following a winter of above-average rainfall. Zonal boundaries are shown in fig. 1. Asterisks denote "not sampled".



H. australis, extended its range downstream a little during the 1973 winter, but this does not seem to be a direct response to salinity changes, in view of the wide tolerances of the species established by Lucas and Hodgkin (1970).

The range of the estuarine barnacle, *Balanus* sp., contracted downstream between the two surveys.

Of the polychaetes studied, only the range of *Ceratonereis erythraeensis* changed between the two summers, expanding upstream. We consider that the distribution of *Mercierella enigmatica* probably remained unchanged between the two summers, despite gaps in the collection records.

Discussion

Though incomplete in many respects, the data presented herein are relatively comprehensive for molluscs, and for this reason the discussion and conclusions will be based largely on molluscan evidence. We recognize that there is an element of uncertainty and subjectivity in some of our assessments of the status of individual species, but nevertheless consider that the information obtained enables some generalizations to be made about the Swan Estuary and its fauna and will assist future studies on environmental and faunal trends.

In all, 97 mollusc species have been recognised as inhabitants, either continuous or temporary, of the Swan Estuary. Within this highly diverse aggregate, four broad groupings may be recognised. These are:

(i) species of marine affinity, with no more than temporary or sporadic estuarine representation — 64 species (66%);

(ii) species of marine affinity, with more or less continuous estuarine representation — 25 species (26%);

(iii) species of exclusively estuarine affinity, having neither marine nor freshwater representation — about seven species (7%); and

(iv) species of freshwater affinity, with limited estuarine and no marine representation — one species (1%).

Species of marine affinity, both continuous and temporary, dominate the mollusc fauna of the Lower Estuary (equivalent to zone 1 on table 2) and in most cases do not extend further upstream. Of the 25 species considered to live continuously in the Lower Estuary, no more than about six seem to be able also to live continuously in the Middle Estuary and only four of these appear to have made temporary incursions in the Upper Estuary during sustained periods of low river discharge. The group is therefore characterised by drastic attenuation above the Lower Estuary; significantly, all of the six species which live continuously in the Middle

Estuary, i.e., *Spisula (Notospisula) trigonella, Tellina (Macomona) deltoidalis, Theora (Endopleura) lubrica, Batillaria (Velacumantus) australis, Nassarius pauperatus* and *N. burchardi*, are much more abundant in this and other estuaries than in normal marine environments. This subgroup of six species stands apart from the others in the fauna in exhibiting a preference for estuarine living, while retaining the ability to inhabit the sea. The presence in the Lower Estuary of such a diversity of marine molluscs (89 species), together with eight echinoderms, an alcyonarian and a scleractinian as as either continuous or temporary inhabitants, demonstrates the distinctiveness of the Lower Estuary as defined here and justifies the three-part biotopic subdivision of the Swan Estuary.

The seven exclusively estuarine species are *Xenostrobus securis, Arthritica semen, Anticorbula amara, Tatea preissi, Potamopyrgus* sp., *Assiminea* sp. and *Hydrococcus graniformis.* These characterise the Middle and Upper Estuaries; the first four are believed to range temporarily into the Lower Estuary in the wake of strong winter flooding. *Potamopyrgus* sp. and *Assiminea* sp., are known only from the Upper Estuary and *H. graniformis* has not been recorded alive from the Swan since about 1840. Despite its presence in the Avon River, *A. amara* is included in this grouping of wholly estuarine species because we consider that this reflects the original relationships of the species in the estuary prior to changes in the hydrology of the Swan-Avon, caused by agricultural practices since the turn of the century. Elsewhere in south-western Australia, the species inhabits estuaries but apparently avoids freshwater tributaries.

The only truly freshwater element, the snail *Plotiopsis australis*, is confined to the higher reaches of the Swan Arm, where it is the sole gastropod.

Over the period covered by our studies, there is evidence that three mollusc species have become established within the Lower and/or Middle Estuaries of the Swan. These are *Spisula (Notospisula) trigonella, Nassarius burchardi* and *Theora (Endopleura) lubrica;* earliest estuarine records are Dec. 1964, Dec. 1965 and Feb. 1973 respectively. We interpret the appearance of these species in the Swan as consequences of transient marine migrations, which by virtue of pre-adaptation to local estuarine conditions, were able to successfully occupy otherwise vacant niches. Conversely, there is reason to suspect that one species, *Hydrococcus graniformis*, has become extinct in the Swan within historic time.

The patterns of response to annual, cyclic environmental changes that are evident from two littoral surveys, one after a series of winters of low rainfall

and relatively high estuarine salinity, the other after a wet winter with a relatively low estuarine salinity are:

(i) the ranges of non-marine species contracted upstream in a period of relatively dry winters and advanced downstream after the next wet winter;

(ii) conversely, the ranges of species of marine affinity extended upstream during a period of dry winters but these extensions did not withstand the next wet winter; and

(iii) by early summer, the larvae of most marine species had successfully recolonised those parts of the estuary upstream where all adults had perished during the previous winter flood.

Conclusions

The Swan Estuary is divisable into three parts on the basis of the distribution of the benthic fauna, particularly the molluscs. The Lower Estuary contains the greatest number of species. Most of these also live in adjacent marine waters and many are believed to invade the Lower Estuary seasonally as planktonic larvae; other marine species inhabit the Lower Estuary more or less continuously and, when conditions permit, invade the Middle and, less often, the Upper Estuaries. Ten mollusc species live continuously in the Middle Estuary, and are uncommon in or absent from the local marine environment. One freshwater species only occurs in the Upper Estuary.

The composition and distribution of the benthic fauna change seasonally, annually and over longer periods. There is a tendency for species ranges to shift upstream in summer and during prolonged dry periods and to shift downstream during the freshwater winter flood. The number of species inhabiting the estuary increases temporarily during summer and over periods of one or more dry winters, when higher estuarine salinities enable marine species to enter the estuary and move upstream. Superimposed on these short-term fluctuations are faunal trends of longer duration, involving the acquisition and loss of species of continuous status within the fauna.

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